

NOTES ON SOME CRITICAL CHARACTERS IN *COLUMNEA* CLASSIFICATION¹

BRIAN D. MORLEY²

Recent workers including Stearn (1969) and Wiehler (1970) have commented on reassessment of some of the sections within *Columnea* sens. lat. The following notes are based on my own attempts at improving *Columnea* classification, and are intended as an evaluation of some of the critical characters employed in the classification.

Columnea belongs to the tribe Columneae, subfamily Gesnerioideae of the Gesneriaceae. The Columneae comprises approximately 396 species of which about 160 belong to *Columnea* sens. lat., the next largest genera being *Episcia* Mart. and *Drymonia* Mart. with approximately 35 species each (Wiehler, 1970). Estimates of the size of *Columnea* sens. lat. vary from 100 plus (Stearn, 1969) to 200 (Willis, 1966). Since *Columnea* was described by Linnaeus in 1753 many new species have been discovered and described with the result that the known variation now exceeds those limits defined by Linnaeus and sometimes borders on those of *Alloplectus* Mart.

Experimental observations on *Columnea* have accumulated in the past 20 years particularly from the disciplines cytology (Eberle, 1956; Fussell, 1958; Sherk, 1960), plant breeding (Sherk & Lee, 1967) and anatomy (Wiehler, 1970). A beginning has also been made on field studies of wild populations in relation to their breeding systems and patterns of variation (Morley, 1968, 1971). These data have not yet been incorporated into the classification of *Columnea* sens. lat. partly because more experimental work is required on larger species samples.

CRITICAL CHARACTERS

Four main types of attribute were used by Hanstein (1865), Bentham and Hooker (1876: 993), and Fritsch (1893–94) to classify *Columnea* sens. lat. These characters were a) corolla morphology, b) calyx morphology, c) leaf anisophylly, and d) leaf vestiture. Each of these characters can be examined on the basis of present knowledge of their variation and their likely evolutionary significance. The possession of a berry fruit serves to distinguish *Columnea* sections from most *Alloplectus*, which have capsular fruits. The Caribbean "*Alloplectus*" species may, for example, relate to sect. *Stygnanthe* or *Collandra* in *Columnea* by having berry fruits. More observations on fruit

¹I wish to thank the Directors at Kew, British Museum, and Glasnevin for the use of herbarium facilities; Dr. W. T. Stearn, the late Mr. C. V. Morton, Dr. A. Skovsted, Mr. B. L. Burtt, Mr. J. P. M. Brenan, and Dr. Walter Lewis for various kindnesses, and Miss Collette Humphries for typing the manuscript so patiently. Part of the study was financed by a Science Research Council Scholarship, London, (1964–67). The author bears sole responsibility for the ideas and opinions given in the article.

²National Botanic Gardens, Glasnevin, Dublin 9, Ireland.



FIGURE 1. Diagrams of corolla morphology, all vestiture omitted. Bar scales = 1 cm.—a. *Columnea aureonitens* Hook. (sect. *Collandra*), cult. Glasnevin.—b. *C. calotricha* Donn. Sm. (sect. *Stygnanthe*) (after A. J. M. Leeuwenberg (1958), *The Gesneriaceae of Guiana*, Fig. 15, p. 385).

characters in *Columnea* and *Alloplectus* are required in cultivation and the field.

1. *Corolla morphology*.—Because *Columnea* is monophyletic on the basis of fruit characters but corolla morphology is diverse, corolla shape is systematically significant and is stressed in the Fritsch and other treatments of the genus. As Macior (1971) has pointed out the “flower as a functional reproductive unit, is an essential link in plant breeding systems,” and, “selection pressure on this link in the breeding system must have a profound influence on speciation and consequently on the principles of systematics of the plant angiosperms, and even of their pollen vectors.” Corolla diversity on *Columnea* sens. lat. is best explained as being the result of past and continuing natural selection pressures exerted by pollen vectors.

While corolla shape is systematically significant it is possible that as a taxonomic suite of characters the attribute could be misleading. We do not yet know whether morphologically similar corollas denote a common evolutionary past or whether convergent evolution might have created similar corollas in species with different origins, as has been suggested in other gesneriads. Increased knowledge of the pollen vectors of *Columnea* will help resolve the question. Little is known about pollination in *Columnea* sens. lat., and it remains to be seen if species are vector specific and which particular species of animal carry out pollination. It may be that the unusually shaped corollas of some columneas such as *C. incarnata* Morton (sect. *Pentadenia*) are adapted to visits by a particular vector such as bats. The changes in corolla morphology which can be brought about by hybridization (Sherk, 1960; Saylor, 1971) should also be remembered, especially as some sections of *Columnea* are genetically crossable.

Pollen-vector selection-pressure on sympetalous corollas determines the amount of dissection and zygomorphy of the organ. This in turn may influence other parts of the flower as is the case in *Columnea* sens. lat. where stamen mechanism changes with increased zygomorphy. Actinomorphy is usually accepted as a less elaborated condition than zygomorphy, and plants with zygomorphic corollas are regarded as derived for the evolution of that organ. Corolla shape in *Columnea* sens. lat. ranges from almost actinomorphic to strongly bilabiate.

i) The most actinomorphic corollas are those of species in sections *Collandra* and *Stygnanthe* (see Figs. 1a–b), these sections being otherwise distinguished by leaf length. The species have corollas which are relatively tough and waxy in texture and which are normally coarsely sericeous or adpressed hairy. It is held (Knuth, 1909: 237) that waxy corolla tissues like those found in *Collandra* and *Stygnanthe* and numerous other columneas are part of an ornithophilous pollination syndrome affording protection to the flowers from the sharp probing bills of feeding birds and rigidity against the buffeting of wing beats. The unfused corolla lobes in *Collandra* and *Stygnanthe* are only several millimetres long, are weakly spreading, and often partly restrict entry to the mouth of the corolla. The corolla tube is usually cylindrical and more or less sigmoid curved in profile, sometimes slightly bulging in the middle, but never ventricose. Like all columneas the proximal end of the tube is more or less gibbous. Some workers suggest that such corollas are hummingbird pollinated, pollen being deposited at the root of the bill, but I have yet to see bird visits.

Because of the narrow throat of sect. *Collandra* and *Stygnanthe* corollas the protandrous stamens, after dehiscence, must make room for the receptive stigma if selfing is to be avoided. The stamen filaments coil up and retract the anthers into the corolla tube, where they can often be found in a moist fungus infected mass. This stamen mechanism can also be seen in corollas of species in sections *Stenanthus* and *Ortholoma*, where the mouth of the corolla is also narrow.

Unlike most cultivated columneas, *C. sanguinea* (sect. *Collandra*) often sets fruit without artificial pollination, and this could indicate that at least some species in *Collandra* are autogamous especially as other collandras such as *C. aureonitens* Hook. also set fruit without artificial pollination in cultivation. *Columnea sanguinea* is a tetraploid.

ii) Increased zygomorphy is seen in the corollas of species in sections *Trichantha*, *Pterygoloma*, *Stenanthus* and *Ortholoma* (see Figs. 2a–d), as slight differences in the length of the free corolla lobes, differences in the relative posture of posterior and anterior lobes the anterior often becoming reflexed, and sometimes by swelling of the corolla tube to a ventricose condition. The pollen vectors of all these sections are not known.

Section *Trichantha* differs from *Stenanthus* and *Ortholoma* in lacking a ventricose corolla tube and sometimes possessing conspicuous appendages of unknown function between the corolla lobes: appendages in the sinuses of the corolla lobes are also known in species from sect. *Collandra*, *C. dissimilis*, and species in sect. *Columnea* has been observed to possess vestigial appendages. Sections *Stenanthus* and *Ortholoma* differ in leaf vestiture. Section *Pterygoloma* corolla shape is intermediate between that of *Trichantha* and *Columnea*. The corolla vestiture of these sections consists of long scattered hairs and is pilose unlike the vestiture of sects. *Collandra* and *Stygnanthe*.

The anthers of the above sections, and those of all columneas, are adherent in two pairs but not fused. Sometimes regarded as a diagnostic character of *Columnea* sens. lat., adherence is by no means a constant feature. Adherence is found when the normal developmental processes of the flower allow its expression, but in poorly developed flowers or ones in the first flush of the season

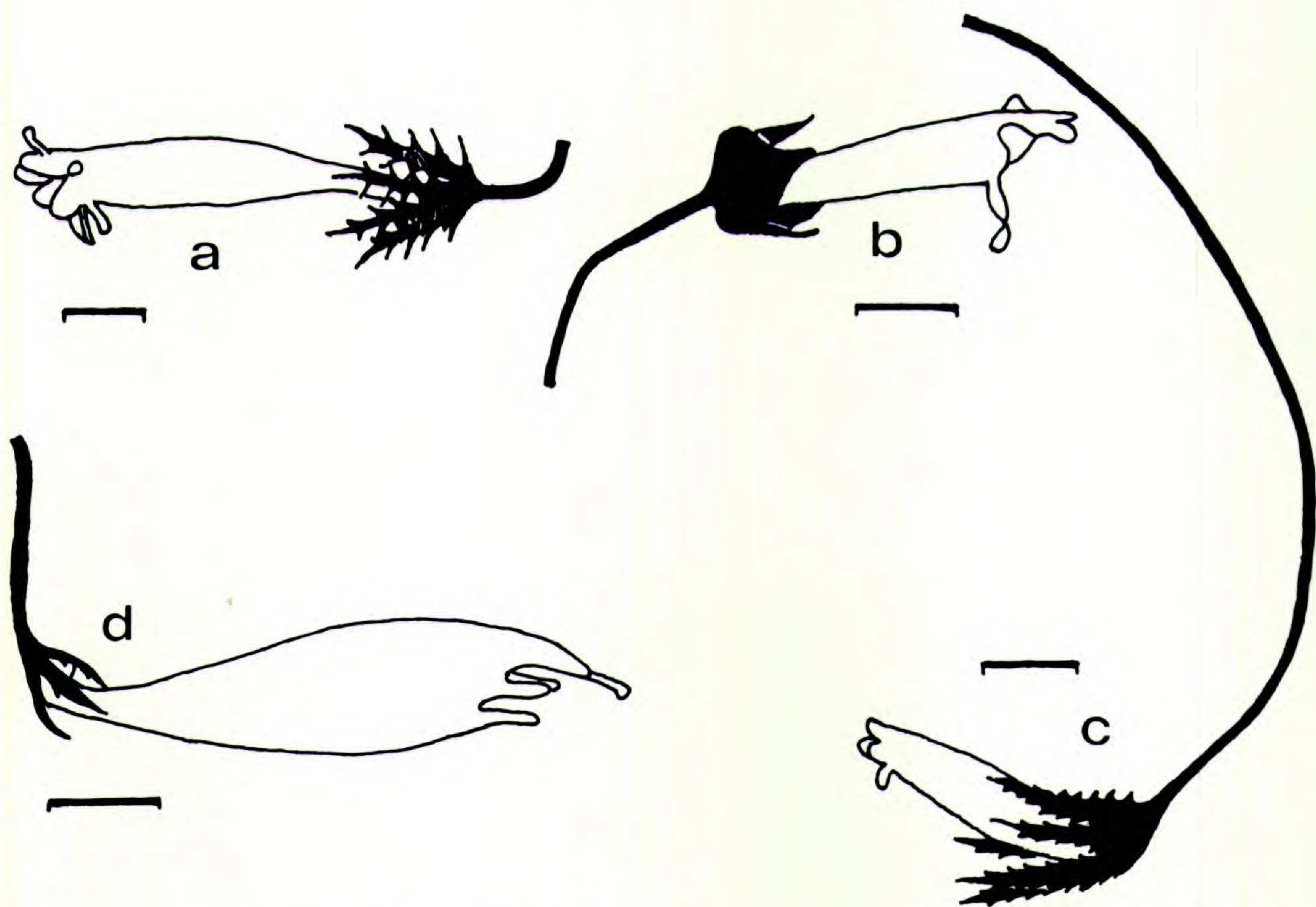


FIGURE 2. Diagrams of corolla morphology.—a. *Columnea elegans* (Rose ex Morton) Morton (sect. *Trichantha*) (after Bot. Mag. t.5428 (1864)).—b. *C. jamaicensis* Urban (sect. *Pterygoloma*), cult. Glasnevin.—c. *C. grata* Morton (sect. *Stenanthus*) (after Oersted 9288, Naranjo, Costa Rica (c)).—d. *C. mira* Morley (sect. *Ortholoma*) (after Dwyer *et al.* 7236, Cerro Jefe, Panama (MO)).

examples are found of free anthers, anthers adherent in twos and threes, or anthers adherent in a linear series of four. The utility of adherence is seen during hummingbird pollination when a more compact and larger surface area of pollen is presented for dusting on the vector than would be available from four free anthers. Adherence also confers more rigidity to the otherwise flexible filaments and assists economical pollen transfer. With minor alterations in detail anther adherence occurs widely in Gesneriaceae.

iii) Extreme zygomorphy exists in sections *Columnea*, *Cryptocolumnea*, and *Pentadenia* (see Figs. 3a–e). The two posterior lobes of the corolla are fused together for much of their length, and the two lateral lobes are variously connate to the posterior lobes. The laterals spread to either side of the corolla or may become reflexed above the posterior lobes. The reflexed or spreading and often narrow anterior lobe of the corolla is the least fused of the five lobes.

Section *Pentadenia* species differ from both *Cryptocolumnea* and *Columnea* in often having long-pedicellate flowers, a corolla tube which is notably ventricose instead of narrowly funnel shaped, and sometimes free corolla lobes which are longer than the corolla tube.

Hummingbirds are known to pollinate some species in sect. *Columnea* (Morley, 1966), and because of similar corolla morphology are presumed to pollinate species in sect. *Cryptocolumnea*. Hummingbirds were the only pollen vectors

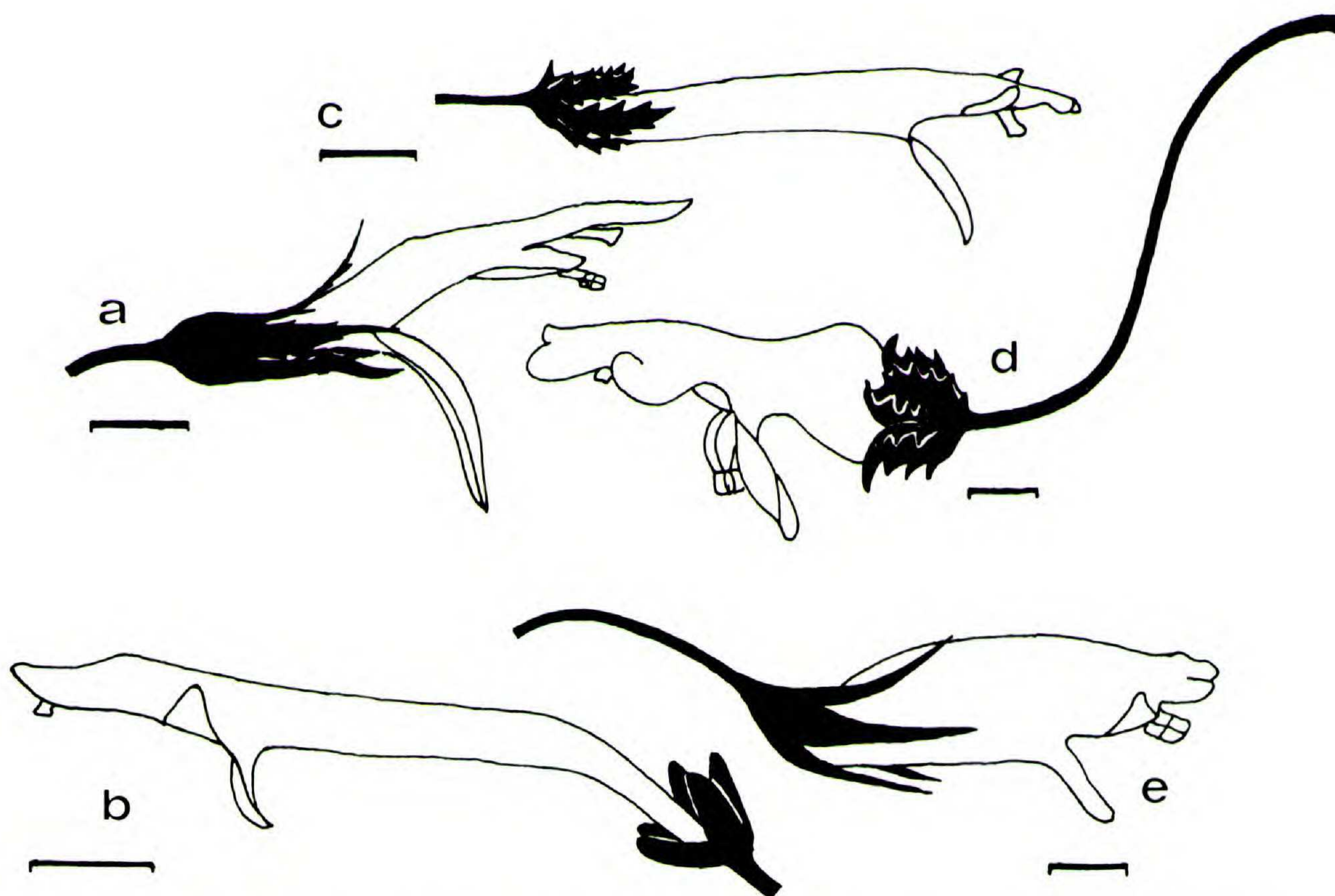


FIGURE 3. Diagrams of corolla morphology.—a. *Columnnea fawcettii* (Urban) Morton (sect. *Columnnea*), cult. Glasnevin.—b. *C. tulae* Urb. var. *tulae* (sect. *Columnnea*), cult. Glasnevin.—c. *C. wilsonii* Wiehler (sect. *Cryptocolumnnea*), cult. Kew.—d. *C. aurantiaca* Decne. ex Planch. (sect. *Pentadenia*) (after Fl. Serres 6: 45, t.552 (1845)).—e. *C. dictyophylla* Donn. Sm. (sect. *Pentadenia*) (after Killip & Garcia 33895, Colombia (us)).

seen to visit the flowers of Jamaican columneas (sect. *Columnnea*), which were the basis for the observations. There are two endemic and therefore resident species of hummingbird in Jamaica, both of which are capable of pollinating columneas. *Trochilus polytmus*, the Streamertail, is the commoner of the two species and the one which was observed to carry out pollination on *C. hirsuta*, *C. urbanii* and two natural interspecific hybrids between *C. urbanii* and *C. rutilans* (Morley, 1971): *Anthracothorax mango*, the Jamaican Mango, is the other bird. The Vervain Hummingbird, *Mellisuga minima* occurs in Hispaniola and Jamaica and is probably too small to work the flowers of columneas in Jamaica (see Table 1).

While the flowers of *Columnnea brevipila*, for example, have corolla tubes which are longer than the average bill length of *Trochilus polytmus*, the nectar may still be accessible if lapped with the tongue, for this organ in *T. polytmus* is almost twice as long as the bill. Birds with bills shorter than the corolla tubes of flowers they are visiting may still bring about pollination.

Trochilus polytmus in Jamaica was polytropic and was seen to visit any nectariferous flower including *Asclepias* (Asclepiadaceae) *Hedychium* (Zingiberaceae), and *Elleanthus capitatus* (Orchidaceae) see Pijl and Dodson (1969: 95). Flower color in sect. *Columnnea* is briefly described by Morley (1973). Jamaican hummingbirds were seen to fly at all levels in the forest canopy and

TABLE 1. Correlation between bill length and corolla tube length in Jamaican hummingbirds and columneas. Bill length was obtained from a sample of skins at the British Museum; corolla tube length from a large sample of herbarium sheets (Morley, 1968); jam. = *C. jamaicensis*, hir. = *C. hirsuta*, faw. = *C. fawcettii*, rut. = *C. rutilans*, arg. = *C. argentea*, urb. = *C. urbanii*, sub. = *C. subcordata*, his. = *C. hispida*, bre. = *C. brevipila*.

Bill length (cm)		Corolla tube length (cm)							
		jam.	hir.	faw.	rut.	arg.	urb.	sub.	his. bre.
<i>T. polytmus</i>	1.8								
<i>A. mango</i>	2.5	2.1	1.9	1.9	1.7	2.4	1.7	2.1	1.5 2.2
<i>M. minima</i>	0.9								

both terrestrial and epiphytic columneas were visited. There was some evidence for hummingbirds remembering a food source.

The vestiture of corollas in sects. *Columnea*, *Cryptocolumnea*, and *Pentadenia* is usually pilose, although species such as *C. nicaraguensis* Oerst. and *C. linearis* Oerst., both in sect. *Columnea*, have sericeous corollas. The behavior of the stamens after dehiscence in these sections, and also *Pterygoloma*, does not involve a direct horizontal withdrawal into the corolla. Instead, anterior corolla dissection allows the filaments to swing through a small vertical arc away from the receptive stigma, after which the withered stamens often dry up resting on the anterior lip. The filaments also coil up a little. Deflection of the anthers from the ripening stigma greatly increases the chances of outcrossing particularly by the activity of pollen vectors such as hummingbirds with bill and head dimensions which correlate with the spatial arrangement of *Columnea* genitalia.

To summarise, the corolla morphology in *Columnea* sens. lat. has a diversity some of the components of which are a) corolla vestiture, b) length of tube, c) width of tube, d) curvature of the tube walls, e) length of the unfused portion, f) relative degree of lobe fusion with one another, g) relative posture of lobes, and h) staminal withdrawal mechanism.

The sections of *Columnea* as shown by corolla morphology must be regarded as parts of the same evolving biological system (see Morley, 1973). The relationship between corolla length and dissection shows a continuum throughout the genus, but it should be remembered that such a correlation involves only two of the several variables which characterise the flowers of these plants, and shows nothing of the development of ventricose as opposed to funnel shaped corolla tubes amongst columneas. The shape of *Alloplectus* corollas could indicate that collandras have common ancestry with alloplecti, and by the same argument columneas sensu stricto could have had stenanthoid or ortholomoid ancestry. However, corolla morphology may have no “phylogenetic” significance, and a trait such as ventricose corolla may be produced by selection for visits by a particular pollen vector. Corolla morphology should be regarded as an integrated system of attributes having the greatest relevance to the reproductive biology of columneas.

2. *Calyx morphology*.—The sepals have been used in *Columnea* classification at sectional, specific, and infraspecific level. The use of the sepals is undisputed

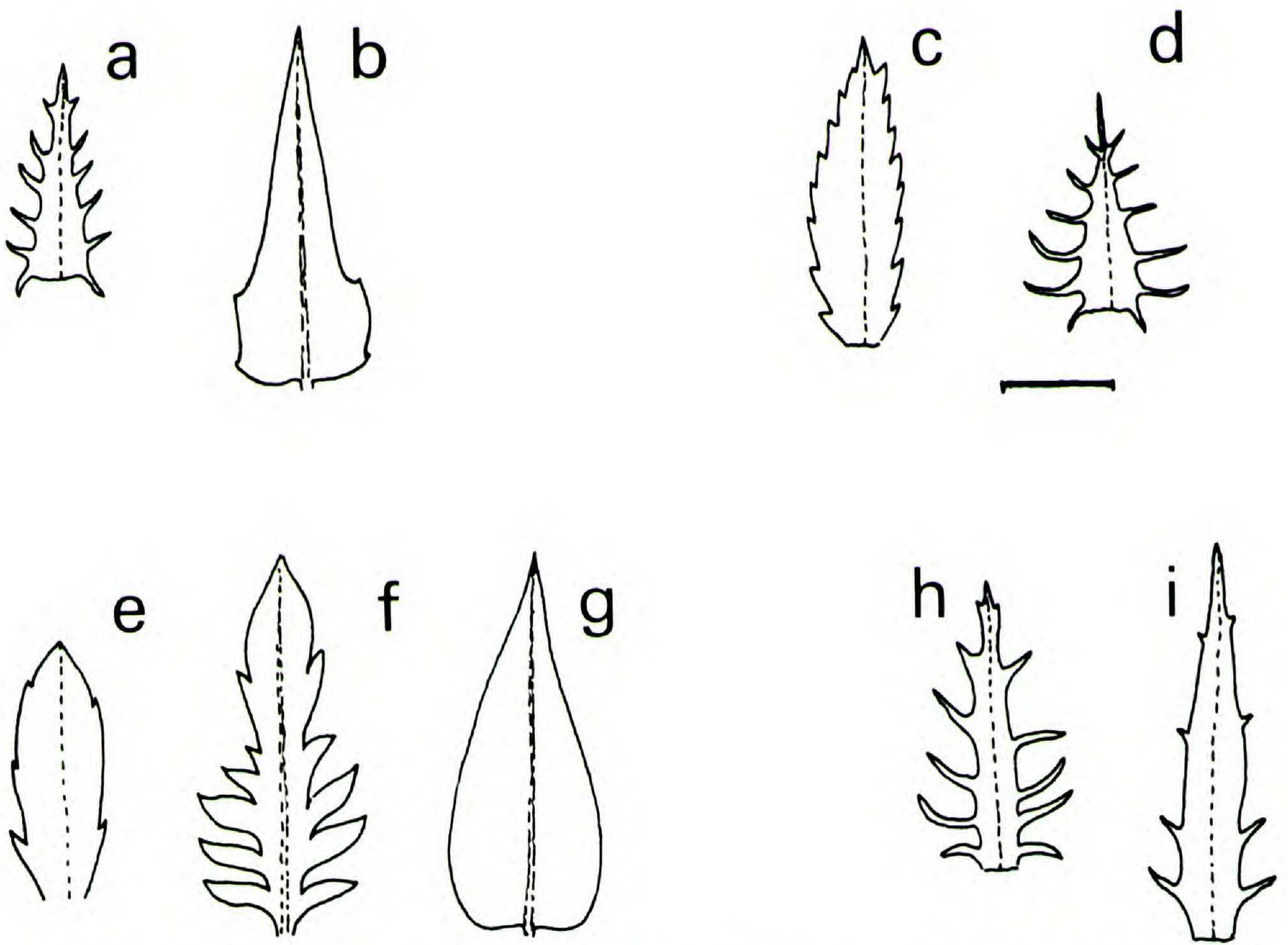


FIGURE 4. Sepal shapes.—a. *Columnnea arguta* Morton (sect. *Columnnea*).—b. *C. allenii* Morton (sect. *Columnnea*).—c. *C. crassa* Morton (sect. *Collandra*).—d. *C. florida* Morton (sect. *Collandra*).—e. *C. tincta* Grisebach (sect. *Columnnea*).—f. *C. rutilans* Swartz (sect. *Columnnea*).—g. *C. nicaraguensis* Oersted (sect. *Columnnea*).—h. *C. moorei* Morton (sect. *Trichantha*).—i. *C. illepida* Moore (sect. *Trichantha*). Bar. scale = 1 cm.

at and below species rank despite the variation of sepal shape and tothing which accompanies the geographical distribution of some species such as *C. scandens* (sect. *Columnnea*) (Morton, 1944; Morley, 1972). At species rank sepal characters largely correlate with other taxonomic and geographic criteria to provide useful distinguishing characters between such species as *C. allenii* and *C. arguta* (both sect. *Columnnea*) and *C. florida* and *crassa* (both sect. *Collandra*) (see Figs. 4 a–d).

Species in sect. *Collandra* have sometimes been noted to possess pectinate sepals, but some species in the group such as *C. consanguinea* have almost entire sepals. The possession of pectinate sepals is supposed to be one of the distinguishing characters between sect. *Stenanthus* and *Ortholoma*, yet in *Stenanthus* not all species exhibit well developed pectinate sepals (e.g. *C. grata*), and the absolute distinctions between poorly pectinate (*C. grata*), pinnatifid (*C. rutilans*, sect. *Columnnea*), and strongly subulate toothed sepals (*C. arguta*, sect. *Columnnea*) are slight.

Although not strictly a morphological character, sepal color must be mentioned. Red sepal colors have been seen to attract hummingbirds to columneas in sect. *Columnnea* in Jamaica. *Trochilus polytmus* was seen to attempt to feed from the red calyces of *C. hirsuta* which had lost corollas and had set no fruit

(Morley, 1968). Red sepals may help to make the flowers more conspicuous to bird pollen vectors especially in species with yellow corollas such as *C. sulfurea*, sect. *Columnea*. The red, reddish, or bronze flower vestiture found in sect. *Collandra* species having otherwise small dull yellow corollas may also attract pollinators. Elaboration of the sepal margin by teeth increases the area of pigment containing-tissue, especially if teeth are pectinate and also covered with long red hairs: to support this notion species having pectinate sepals also have red sepals (e. g. *C. sanguinolenta*, sect. *Stenanthus*, and *C. major*, sect. *Trichantha*). The red pigment found in flowers and leaves of some columneas is a 3-desoxyanthocyanin, called columnin.

Sepal color may also serve to attract fruit dispersal agents. At fruiting time the white, pink, red, or magenta berries of columneas are about 1 cm. diameter, and when surrounded by brightly colored sepals, possibly with an elaborated margin such as in *C. rutilans* (sect. *Columnea*), the fruits are made more conspicuous for dispersal agents than if the sepals are green or chaffy and withered. The fruits are widely presumed to be bird dispersed, but no observations of the process have yet been made: secondary agents are ants (Morley, 1968). Ridley (1930: 392, 410, 418) notes that the combination of red and white colors is often associated with bird dispersal of fruits, and this color combination is more or less expressed in a majority of columneas studied. Fruits may be white or pink with red sepals (e. g. *C. schiedeana*, sect. *Columnea*) or red with pale chaffy sepals (*C. tulae*, sect. *Columnea*). In *C. harrisii*, sect. *Columnea*, having green sepals at flowering time, there is a slight development of red pigmentation after the corolla withers and before the fruit reaches maturity, indicating that sepal coloring in at least this species is correlated with fruiting time. Species such as *C. florida*, sect. *Collandra*, do not have a red-white combination of fruiting colors, the sepals being colored orange and fruits yellow to orange. The berries of Jamaican columneas are slightly sweet to human taste but very seedy, and the matrix of the berry sticky.

In summary calyx characters are useful at species level but questionable at sectional level, partly because variation of sepal characters can be as great within sections as between. It is suggested that sepal shape, margin type, and color have the dual role of attracting pollen vectors during flowering, and later helping attract fruit dispersal agents.

3. *Leaf anisophylly*.—Leaf anisophylly has been used as a reliable taxonomic character in *Columnea* classification, because herbarium sheets give an impression that the character provides a morphological discontinuity between species. This is so with certain species but cannot be said for all columneas.

Sherk (1960) explained variation of anisophylly in *C. nicaraguensis* and *C. verecunda* (both sect. *Columnea*) as due to genetic heterozygosity for leaf size and shape on the basis of selfing experiments, hence implying some genetic basis for the taxonomic character anisophylly. My observations on species with weakly anisophyllous shoots, and which thus resemble some of the species studied by Sherk, show that phenotypic variation can destroy the value of anisophylly as a taxonomic character.

In all columneas the arrangement of leaves about the axis partly depends

TABLE 2. Alterations of leaf anisophylly with shoot inclination in *Columnea*. Leaf pair ratio (LPR) is an expression of the amount of anisophylly obtained by dividing the length of the short leaf into that of the longer for each pair (an LPR = 1.0 is isophyllous).

Species	Average leaf pair ratio		Sample number of nodes	
	Erect	Horizontal	Erect	Horizontal
<i>C. rutilans</i>	1.4	2.0	11	11
<i>C. fawcettii</i>	1.5	1.9	14	14

on inclination of the shoot to a source of light and partly on the genotypic length and breadth of the leaf of the particular species. Variation of leaf dimensions I regard as due to polygenic inheritance. Alterations of leaf posture are seen to be brought about by resupination of petioles in agreement with the observations of Goebel (1900: 113) and Hill (1939). An axis oriented parallel to a source of light has leaves arranged in a radial leaf mosaic around the axis, but one oriented at right angles to a source of light has leaves in a dorsiventral "frondlike" leaf mosaic which is often apparent in herbarium specimens. Simultaneous with changes in the leaf arrangement about the axis are changes altering the final expression of leaf length and breadth of pairs of leaves at nodes where leaf expansion is still active. The changes of leaf size appear to be related to axis orientation and how pairs of decussate leaves can be best arranged for maximum light interception. Table 2 shows the effect of axis orientation on anisophylly for two pairs of shoots of well grown *C. fawcettii* and *C. rutilans* (both sect. *Columnea*) in cultivation in a controlled environment. Care was taken to sample nodes of comparable age, as LPR in Jamaican species was found to stabilize only after the tenth node had been produced. The average LPR for *C. fawcettii* is 1.9 based on a sample of 68 herbarium specimens, figures which indicate that in nature the shoots are horizontally pendent when mature as is confirmed in the field. *Columnea rutilans* had an LPR of 2.5 in nature based on 48 herbarium specimens, a figure larger than the LPR achieved in experiment.

Columnea microphylla (sect. *Columnea*) with leaves less than 1.0 cm long is always isophyllous (LPR = 1.0) irrespective of whether shoots are pendulous or prostrate because pairs of leaves are small enough to find accommodation at each node without lamina overlap. Anisophylly is also less marked in narrow leaved species such as *C. crassifolia* and *C. linearis* (both sect. *Columnea*) as might be expected because narrow leaves can also be accommodated in both erect and horizontal shoot positions without lamina overlap if slight resupination occurs. It is in large leaved species such as *C. purpurea* (sect. *Collandra*) or *C. wilsonii* (sect. *Cryptocolumnea*) that some physical change in the size of leaves at each node must occur if lamina overlap is to be avoided: there seems to be strong genetic control over leaf anisophylly in large leaved species on the basis of constancy of anisophylly in these plants. In comparison with *C. microphylla* the LPR of *C. sanguinea* (sect. *Collandra*) is 6.0–6.5. The taxonomic significance of this reasoning is that as LPR approaches unity, the effects of phenotypic variation may be enough to spoil that anisophylly which has a genetic

TABLE 3. Leaf pair ratio in Jamaican columneas showing sample size and standard deviation. Sample size refers to number of herbarium specimens from which a single node was examined; and hir. = *C. hirsuta*, faw. = *C. fawcettii*, rut. = *C. rutilans*, arg. = *C. argentea*, sub. = *C. subcordata*, urb. = *C. urbanii*, har. = *C. harrisii*, bre. = *C. brevipila*, his. = *C. hispida*, jam. = *C. jamaicensis*, pro. = *C. proctorii*.

Species	hir.	faw.	rut.	arg.	sub.	urb.	har.	bre.	his.	jam.	pro.
Mean LPR	1.8	1.9	2.5	1.5	3.5	1.3	3.6	1.2	3.3	1.5	3.5
Sample size	43	68	48	11	14	27	9	17	6	21	16
Standard deviation	0.5	0.6	0.9	0.4	1.0	0.3	1.2	0.2	1.5	0.3	1.2

component and which is being used as a taxonomic character. Table 3 shows LPR for Jamaican columneas and the amount of variation of values for each species all of which belong to sect. *Columnea* except *C. jamaicensis* (sect. *Pterygoloma*). It is suggested that any *Columnea* having leaf dimensions of this magnitude will behave in the same way despite its geographical origin or taxonomic affinity.

It may be useful to speculate on correlation between leaf size and ecological adaptation in columneas, although little ecological work has been carried out on this group with versatile terrestrial and epiphytic preferences. Large leaved species with laminas 20–30 cm long have leaves which are relatively thin in proportion to area, which implies a possible susceptibility to wilting from transpiration losses. If Wiehler’s observations of 1970 are general for all columneas, the fact that large leaved species have smaller more numerous epidermal cells per square centimetre than small leaved suggests that large leaved species also have more stomates per unit area. This would support the notion that large leaved species are susceptible to transpiration losses resulting in serious wilting. While needing much investigation, the habitat requirements of large leaved species may approximate to sheltered niches, where leaves suffer little wind damage, moist niches where transpiration can be made good by water uptake or where transpiration will be minimal, and perhaps shady niches where light intensity requires large surface areas in leaves for photosynthesis to proceed satisfactorily. These conditions are indicated on some herbarium sheets. Large leaved taxa require relatively thick axes (10–15 mm diameter) to support the foliage, and such heavy plants may be better fitted to terrestrial niches, although herbarium sheet data indicate that a number of large leaved taxa are regularly epiphytic.

Small leaved species with laminas to 3.0 cm long have leaves thicker in proportion to area and also have fewer larger epidermal cells. These attributes suggest that small leaved species are found in more dry, windy, sunlit epiphytic habitats, where water stress can be offset by the development of succulence in the leaves, and where the thin axes having a pendulous or drooping habit both weigh little and support the leaves. These conclusions are borne out by field observations and herbarium sheet data. Wiehler (1970) found water storage tissues in *Columnea* leaves and Morley (1968) found that in Jamaican columneas all of which possess water storage in the leaves, the thickness of storage tissue

is closely related to altitudinal distribution and wetness of habitat in at least *C. hirsuta* and *C. fawcettii* (sect. *Columnea*) (Morley, 1972.) Specialised ecological adaptation can be interpreted from the habit and foliage of species such as *C. allenii* or *C. arguta* (sect. *Columnea*), both being well suited to an epiphytic niche, and they show a narrow tolerance to water and temperature regime experienced in cultivation in support of their being ecologically specialized. In contrast, one finds that *C. sanguinea* (sect. *Collandra*) seems able to accommodate to a range of water and temperature regimes in cultivation, perhaps indicating less ecological specialization.

Conclusions on leaf anisophylly are that when LPR is large the character is sufficiently stable for the definition of groups. This is the same as saying that long, broad leaves are a useful character in the classification of columneas.

4. *Leaf vestiture*.—There are four types of hairs in columneas studied, a) multicellular sharply pointed, b) multicellular gland-tipped, c) multicellular slender, and d) glandular papillae. This largely agrees with Wiehler (1970), who does not recognise the different thickness of hair types a) and c), the latter being found only on corollas and some leaves of species with densely sericeous vestiture. The walls of the cells are refractive and clear or brownish, but the cell cavity may be clear or filled with various amounts of the red pigment columnin.

There are large numbers of possible combinations and permutations of different hair types, in various postures and with various densities on the adaxial and abaxial leaf surfaces, which are not necessarily the same. It has been found that particular vestitures characterize particular species with the greatest accuracy in herbarium studies, and inheritance of posture, density, and type of hair is documented for some species (Morley, 1971): in hybrids the vestiture characters may show heterosis.

As stomates are confined to the abaxial leaf surface in the columneas so far examined, adaxial leaf vestiture cannot serve to reduce transpiration. It has been suggested that vestiture may reduce the amount of light entering the leaf, or even increase light admitted. Colored leaf vestiture may serve to attract pollinators to the flowers of species in sections *Ortholoma* and *Collandra*, perhaps in conjunction with the red blotching on the undersides of leaves of species in the above sections and also *Cryptocolumnea* and *Pentadenia*. Seen from below the foliage, where the flowers tend to hang and from which direction birds generally approach the flowers, the red pigmentation on leaves of species such as *C. sanguinolenta* (sect. *Stenanthus*) or *C. sanguinea* (sect. *Collandra*) is most conspicuous.

Leaf vestiture has been used to distinguish between sections *Stenanthus* and *Ortholoma*, but when the same attributes which define these sections appear in *C. florida* and *C. pectinata* (sect. *Collandra*), it is given the importance of denoting only specific difference; clearly such use of characters is arbitrary. This does not detract from the usefulness of leaf vestiture at species level.

CYTOLOGY AND GENETICS

An interesting relationship exists between the corolla morphology and inter-fertility data so far available for *Columnea* sens. lat. (Morley, 1973). Hybrids

between species in sect. *Collandra* and *Stenanthus* form stainable pollen, but sect. *Collandra* species will not produce hybrids forming stainable pollen when crossed with sect. *Columnea* species. Sections *Trichantha* and *Pterygoloma* (Saylor, 1971) are both compatible with sect. *Columnea*, but *Trichantha* and *Pterygoloma* produce no stainable pollen when crossed. Section *Trichantha* crossed with *Ortholoma* species and crossed with *Stenanthus* species both result in hybrids which form stainable pollen. Hybrids between *Columnea* and *Cryptocolumnea* sections form stainable pollen. Such breeding relationships suggest that section *Collandra* and *Columnea* are the most genetically dissimilar, with sections *Ortholoma*, *Trichantha*, *Stenanthus* and *Pterygoloma* genetically intermediate. This is precisely what is shown by corolla morphology where *Collandra* and *Columnea* corollas occupy opposite poles of a scatter diagram for corolla length against corolla dissection, and the remaining sections occur in between the two (Morley, 1973). This relationship may suggest that corolla morphology is taxonomically reliable as a character and is more than simply an indicator of the type of pollinator visiting a species.

LITERATURE CITED

- BENTHAM, G. & HOOKER, J. D. 1876. *Columnea*. In "Genera Plantarum." Vol. 2.
- EBERLE, P. 1956. Cytologische Untersuchungen an Gesneriaceen I. Chromosoma 8: 285–316.
- FRITSCH, K. 1893–94. Gesneriaceae. In A. Engler & K. Prantl, "Die natürlichen Pflanzenfamilien." 4(3b): 133–185.
- FUSSELL, C. P. 1958. Chromosome numbers in Gesneriaceae. Bailey 6: 117–123.
- GOEBEL, K. 1900. Organography of Plants. Oxford.
- HANSTEIN, J. 1865. Die Gesneraceen des Königlichen Herbariums und der Gärten zu Berlin. . . . II. Abschnitt Drittes Stück. Linnaea 34: 225–446.
- HILL, A. W. 1939. Resupination studies of flowers and leaves. Ann. Bot. (London), n.s. 3: 871–888.
- KNUTH, P. 1909. Handbook of Flower Pollination. Vol. 3. Oxford.
- MACIOR, L. W. 1971. Coevolution of plants and animals—Systematic insights from plant-insect interactions. Taxon 20: 17–28.
- MORLEY, B. D. 1966. *Columnea* and aspects of its evolution. Science notes and news (Jamaica) 2(4): 13–14.
- . 1968. Biosystematics of *Columnea* in Jamaica. Thesis, University of the West Indies, Mona, Jamaica.
- . 1971. A hybrid-swarm between two hummingbird pollinated species of *Columnea* in Jamaica. Bot. Jour. Linn. Soc. 64: 81–96.
- . 1972. The distribution and variation of some gesneriads in Caribbean islands. Pp. 239–257, in D. H. Valentine (editor), "Taxonomy, Phytogeography and Evolution." London.
- . 1973. Ecological factors of importance to *Columnea* taxonomy.
- MORTON, C. V. 1944. The West Indian species of *Columnea*. Contr. U. S. Natl. Herb. 29: 1–15.
- PIJL, L. VAN DER & DODSON, C. H. 1969. Orchid Flowers, their Pollination and Evolution. Coral Gables, Florida.
- RIDLEY, H. N. 1930. The Dispersal of Plants throughout the World. Ashford.
- SAYLOR, W. R. 1971. Gesneriad cross roads. Gloxinian 21: 30.
- SHERK, L. C. 1960. Cytogenetic studies in *Columnea* L. Thesis, Cornell University, Ithaca.
- & LEE, R. E. 1967. Interspecific hybridization in the genus *Columnea* (Gesneriaceae). Bailey 15: 89–96.
- STEARNS, W. T. 1969. The Jamaican species of *Columnea* and *Alloplectus*. Bull. Brit. Mus. Nat. Hist. (Bot.) 4: 181–236.
- WIEHLER, H. 1970. Studies in the Gesneriaceae-Gesnerioideae. Thesis, Cornell University, Ithaca.
- WILLIS, J. C. 1966. A dictionary of the Flowering Plants and Ferns. Ed. 7. Cambridge. Pp. 265–281, in V. Heywood (editor), "Taxonomy and Ecology." London.